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SONG IN THE WHITE-EYED VIREO

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ABSTRACT.—This is an audiospectrographic study of the primary song of the White-eyed Vireo (*Vireo griseus*) based on 16,612 recorded songs of 379 birds from 20 states, Bermuda, and the Bahamas, and representing the five subspecies that occur in the United States. Information is given on song construction, song variation, individual repertoires, singing behavior, song and note type sharing by two or more birds, and geographic variation. The largest song-type repertoire was 17, and most birds had a repertoire of 10 to 14 song types. In most birds represented by a sizeable number of songs, even in well studied areas, a few of the individual's song types were unique (found in no other bird studied), and the rest were shared by other birds; this sharing was with more birds outside the area than in it, with one or more song types occurring in birds several hundred kilometers away. The 614 song types found were classified in five major groups; the incidence of the types in these groups, as well as the song length and the number of notes in the song, varied geographically.
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The songs of a White-eyed Vireo (*Vireo griseus*) are short, and they generally begin and end with a short sharp note; the other notes of the song may be buzzy or musical, and are usually slurred. A common song of this vireo might be paraphrased as "pick-up-the-beeer-check." The songs vary; while different birds, sometimes many kilometers apart, may sing a given song type, songs of different birds are often different.

This paper examines variations in songs of birds from different parts of the United States. I am concerned here solely with primary song (termed "discrete" song by Bradley 1980, 1981), although I have examined recordings containing calls, rambling song, chatter, and sub-song.

Bradley (1981), studying song variation in a local population, based his conclusions on similarities in the notes or elements of the songs. My study is similar, but is based on song types as well as individual notes, and is based on more birds, from different parts of the country.

METHODS AND MATERIALS

I have examined 463 recordings of White-eyed Vireo song, believed to represent 379 birds (see Tables 1 and 2). Most of these recordings were made by me and are housed in the tape collection of the Borror Laboratory of Bioacoustics, Ohio State University, but I have been provided with copies of recordings from the following people and institutions: Richard A. Bradley (48 recordings), Cornell Laboratory of Ornithology (36 recordings), Florida State Museum (12 recordings), Sam Houston State University (10 recordings), and North Carolina State Museum (6 recordings).

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TABLE 1
DATA ON SONG AND NOTE TYPE UNIQUENESS

Area or subspecies[a]	No. of birds	No. of songs	Song types: Total found[b]	Song types: Found in only 1 bird: No.	Song types: Found in only 1 bird: %	Note types: Total found[b]	Note types: Found in only 1 bird: No.	Note types: Found in only 1 bird: %
Ohio areas								
Cast	10	332	28	8	29	63	0	0
DWA	6	176	19	7	37	54	1	2
Hb	8	1345	46	17	35	74	1	1
BW	14	1633	49	20	41	84	3	4
DCP	12	443	42	22	52	75	1	1
CCV	35	1100	46	8	17	80	0	0
ZSF	35	3822	80	27	34	88	4	5
BOSP	10	986	40	11	28	65	1	2
SSF	29	1817	65	19	29	90	2	2
Total	159	11,654	221[b]	139	63	135[b]	13	10
All Ohio	186	12,021	235	154	66	142	13	9
novaboracensis	211	12,368	267	183	69	166	19	11
griseus	124	3371	267	206	77	264	51	19
maynardi	26	519	50	46	92	147	30	20
bermudianus	1	21	6	6	100	23	4	17
micrus	17	327	31	29	94	91	14	15
All birds[c]	379	16,612	614	470	77	375	118	32

[a] Abbreviations for the Ohio areas are explained in the text.
[b] Number of different types.
[c] Seven song types were found in two subspecies. Three note types, AA (the final note in song 7) (Fig. 1), CC (the first note in song 4) (Fig. 1), and PC (the first note in song 21) (Fig. 2), were found in all five subspecies, 35 were found in four subspecies, and many were found in two or three subspecies.

To obtain as much as possible of each bird's song-type repertoire, I recorded for 1–2 min (if the bird changed song type during this time I continued recording for another 1–2 min), then stopped and waited until the bird changed songs before continuing the recording. If a bird stopped singing I played back to it some songs of this species; this usually started the bird singing again. On subsequent visits to the bird's territory, if the bird was not singing when I arrived, I used playbacks to start it singing.

The playbacks used in the field were of three types: one (song 46, Fig. 3) a type found in only one bird studied, another (song 1, Fig. 1) found in 29 birds, and the third (song 2, Fig. 1) found in 41 birds. The three types proved equally effective in inducing singing, and the songs sung by the birds involved differed on different occasions.

I made sonagrams of each song type in each recording with a Sona-Graph 7029A, using the wide band setting. Time and frequency scales were obtained from the Sona-Graph, and note and song lengths were measured on the graphs to the nearest 0.01 sec. Individual birds were assigned numbers.

Many localities are represented in the material studied, but the following Ohio areas, where much of my recording was done, are referred to by abbreviations: BOSP—Burr Oak State Park, Morgan County (6 seasons); BW—Blendon Woods Metro Park, Franklin County

TABLE 2
DATA ON SONG LENGTH AND NOTE CONTENT

Subspecies	Location	No. of birds	No. of songs	Song length (sec)[a]		No. of notes in song[a]	
				Range	Mean[b]	Range	Mean[b]
novaboracensis	CT, NY, NJ, PA, OH, IN, IL, NB,	195	12,116	0.24–2.42	1.13 ± 0.003	1–17	8.19 ± 0.02
	WV, KY, TN, NC, AL	16	252	0.40–1.58	1.08 ± 0.02	2–14	8.21 ± 0.14
	Total	211	12,368	0.24–2.42	1.13 ± 0.003	1–17	8.19 ± 0.02
griseus	MD, VA, NC, SC, GA	22	356	0.44–1.83	0.97 ± 0.01	2–16	7.44 ± 0.11
	Gainesville, FL	46	1799	0.42–2.30	1.05 ± 0.005	2–17	7.40 ± 0.05
	FL Panhandle	41	892	0.60–2.11	1.05 ± 0.01	3–15	7.30 ± 0.06
	LA, central TX	15	324	0.63–1.79	1.15 ± 0.02	4–18	9.16 ± 0.15
	Total	124	3371	0.42–2.30	1.05 ± 0.004	2–18	7.55 ± 0.04
maynardi	South FL, Bahama	26	519	0.58–1.38	0.94 ± 0.01	3–13	6.49 ± 0.08
bermudianus	Bermuda	1	27	0.90–1.73	1.17 ± 0.03	4–8	6.70 ± 0.21
micrus	South TX	17	327	0.65–1.38	0.90 ± 0.01	4–13	7.19 ± 0.21
All birds		379	16,612	0.24–2.42	1.10 ± 0.002	1–18	7.98 ± 0.02

[a] Based on all songs studied.
[b] $\bar{x} \pm$ SE.

(12 seasons); Cast—Resthaven Wildlife Area, Castalia (8 seasons); CCV—Clear Creek Valley and vicinity, Hocking and Fairfield Counties (20 seasons); DCP—Darby Creek Metro Park, Franklin County (10 seasons); DWA—Delaware Wildlife Area, Delaware County (5 seasons); Hb—Highbanks Metro Park, Delaware County (4 seasons); SSF—Shawnee State Forest, Scioto County (12 seasons); and ZSF—Zaleski State Forest, Vinton County (10 seasons).

The term "note" is used in this paper for an individual unit of sound, and is represented on a sonagram by a continuous mark, or by two or more marks that overlap in time; the term "song type" is used for a particular sequency of notes making up a song; other terms in the literature for song type are motif or theme (Baptista 1976), song pattern (Marler and Isaac 1961), or simply "song" (Thorpe 1961).

Anyone attempting to recognize note or song types in a bird's vocalizations always faces the problem of how different notes or songs must be to be considered different types, or how much notes or songs may differ and still be recognized as the same type. Any criteria one may use will always be subjective, and different people designating types in the same vocalizations might recognize different numbers of types. No matter what criteria one uses, he will always encounter situations where he has a problem deciding where to draw the line between different types, and any conclusions drawn regarding these types may have to be weighed against the validity of the type designations. In the case of note types, in my study of Bradley's Gainesville, Florida, birds I recognized 149 different note types, whereas Bradley recognized 150, which would suggest that perhaps my note-type designations are reasonably valid.

RESULTS

Song Construction

The notes in a White-eyed Vireo song range in length from less than 0.01 sec to 0.70 sec ($\bar{x} = 0.095 \pm 0.001$ sec [SE]), in frequency from about 1.6 to 8.5 kHz, and in quality from pure tones to harsh or buzzy notes with a pitch range of an octave or more. Most notes are slurred, some over an octave or more in one or two hundredths of a sec. The modulation rate in most buzzes is under 150/sec, but in some may be as high as 350/sec. Most songs begin and end with a short, abruptly slurred note (usually slurred over an octave or more), but there is no definite sequency of the other notes in the song. Some songs contain a rapid series of similar notes, often of decreasing pitch, giving the effect of a short trill or sputter; such a series may be anywhere in the song. About half the notes are ≤ 0.05 sec; about half of the birds studied had long notes (≥ 0.3 sec) in their repertoire, but only 5% of the notes in the songs studied were this long (Table 3). Occasionally a note may be uttered two or more times in succession, or may appear in different parts of the same song.

Each bird's repertoire of note types is used to produce a variety of song types; a given note or note sequence may be used in different parts of different song types. The 45 birds that were represented by over 100 songs each had repertoires of 28 to 54 ($\bar{x} = 42.9$) note types. There was a significant positive correlation in these 45 birds ($r = 0.7413$, $P < 0.001$) between the number of song types and the number of note types. A given

Table 3
Song Length in the White-eyed Vireo

Subspecies	Location	No. of notes studied[a]	Note length (sec)	% of the note types of different duration (sec)			% of birds with long notes[c]	% of notes that were long[c]
				≤0.05	0.051–0.10	>0.10		
novaboracensis	CT, NY, NJ, PA, OH, IN, IL, NB,	4206	0.10 ± 0.002	50.9	14.4	34.8	62.6	5.9
	WV, KY, TN, NC, AL	190	0.08 ± 0.006	55.3	18.4	26.3	50.0	4.7
	Total	4396	0.10 ± 0.002	51.0	14.6	34.4	61.6	5.8
griseus	MD, VA, NC, SC, GA	241	0.09 ± 0.006	44.8	24.1	31.1	27.3	2.9
	Gainesville, FL	985	0.10 ± 0.003	43.8	19.0	31.2	54.3	3.7
	FL Panhandle	545	0.09 ± 0.004	43.5	26.6	29.9	43.9	5.0
	LA, central TX	229	0.08 ± 0.005	54.1	21.8	24.0	20.0	1.3
	Total	2000	0.09 ± 0.002	45.0	22.0	33.0	41.9	3.7
maynardi	South FL, Bahama	306	0.91 ± 0.005	43.5	25.5	31.0	41.9	3.7
bermudianus	Bermuda	24	0.11 ± 0.017	33.3	33.3	33.3	0	0
micrus	South TX	182	0.08 ± 0.006	52.2	22.0	25.8	29.4	2.7
All birds		6908	0.10 ± 0.001	48.9	17.5	33.6	51.5	5.0

[a] The totals of the number of note types for each bird studied.
[b] $\bar{x} \pm$ SE.
[c] Long notes = >0.3 sec; the number of birds studied in the different areas is given in Table 2.

note in these 45 birds was used in 1–11 ($\bar{x}$ = 2.0) different song types, and 31.3–73.0% ($\bar{x}$ = 46.1%) of the note types were used in only one song type. The number of notes in the songs varied from 1 to 18 (Table 2).

Song Types

The different utterances of a given song type by a given bird were usually almost identical. There were a number of cases in the songs studied where a song type (of an individual bird) was represented by two or more variations—usually in where, along a particular sequence of notes, the song ended, or in the number of times a note was repeated (where note repetition occurred). Only rarely was there variation in how the song began (in songs of a given sequence of notes).

I recognized 614 song types in the songs studied, and in classifying these I used as the primary basis the least variable part of the songs, the beginning. Two songs were considered to be different types if they began differently, or if they contained different note types. As with note types, one will always encounter problems in deciding where to draw the line between different song types, especially when dealing with songs of different birds, but I believe my song-type designations are reasonable. Some of the figures (e.g., songs 30–32, Fig. 3) illustrate what I consider to be the same song type sung by different birds.

I arranged the song types of this vireo, based on how the songs began, in five major groups:

Group 1.—Songs beginning with 2 to 6 short notes of decreasing pitch, these notes somewhat similar to the call of a Summer Tanager (*Piranga rubra*) (songs 1, 19, 22, 30, 31, 32; cf. 43–45) (Figs. 1–3).

Group 2.—Songs beginning with two or more repetitions of a particular note (songs 15, 20) (Fig. 2).

Group 3.—Songs beginning with a hoarse or buzzy note, this note short and containing frequencies ranging over an octave or more (songs 12, 21, 25) (Figs. 1, 2).

Group 4.—Songs beginning with a short, sharp, musical note, this note abruptly slurred over an octave or more (songs 2–3, 5–11, 13–14, 16–18, 23–24, 33–40) (Figs. 1–3).

Group 5.—Songs beginning with a long note, this note either buzzy or musical, and its frequencies ranging over less than an octave (songs 4, 41, 42) (Figs. 1, 3).

Each of these five major groups was further subdivided, with a total of 59 subgroups; each subgroup was designated by one or two letters, and the types in each subgroup were numbered. Each song type was designated by a number-letter-number combination; e.g., type 4bc–13 (song 14, Fig. 2) was the thirteenth type in major group *4*, subgroup *b*, sub-subgroup *c*.

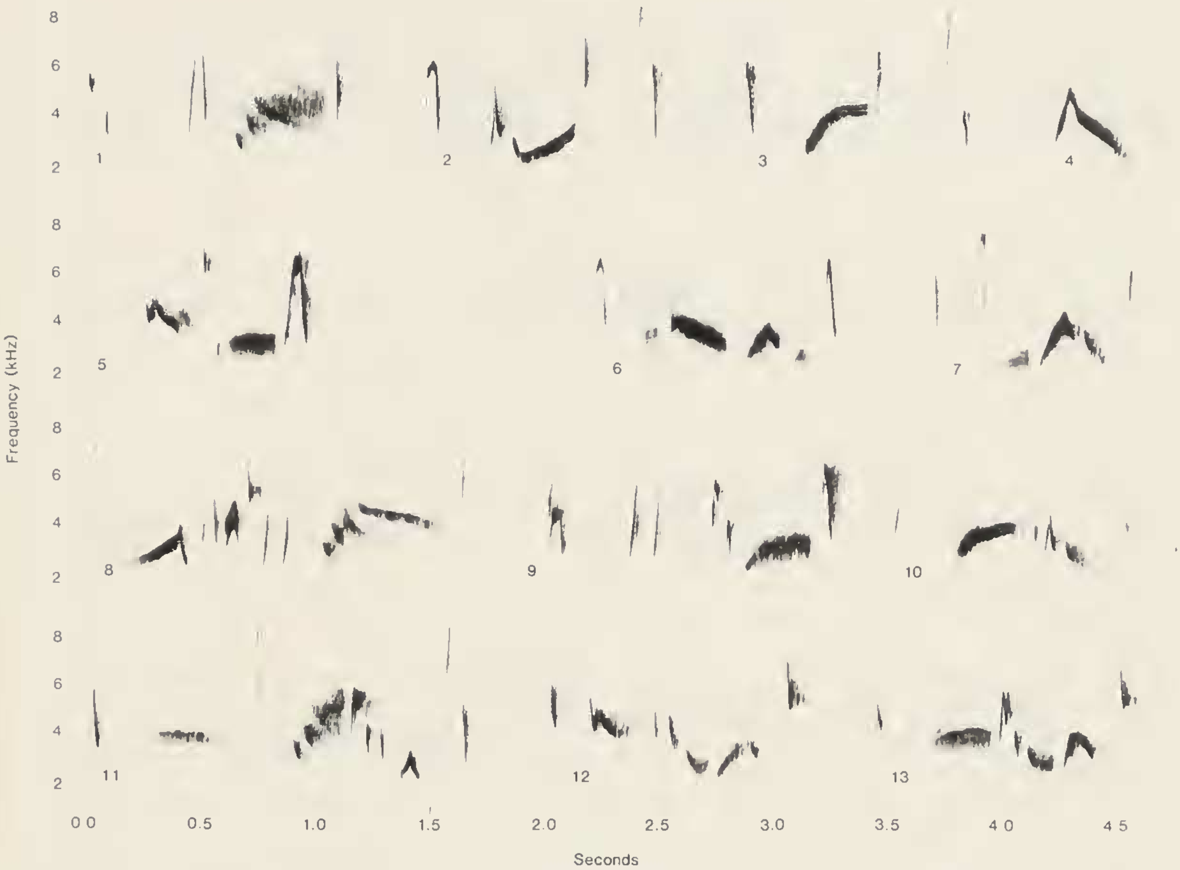

FIG. 1. Sonagrams of the 13 song types of White-eyed Vireo No. 101, Zaleski State Forest, Vinton County, Ohio, June 1980. The numbers in parentheses (in this and the other figure captions) are the number of the recording, and the song in the recording, from which the sonagram was made. Song 1.—Type 1a-9 (15558-13); found in 29 birds, Ohio and southwestern Kentucky. Song 2.—Type 4e-22 (15558-27); found in 41 birds, Ohio, Indiana, and West Virginia. Song 3.—Type 4bc-10 (15558-31); found in 21 birds, Ohio (Lake Erie to the Ohio River). Song 4.—Type 5aa-1 (15558-42); found only in this bird. Song 5.—Type 4c-26 (15558-32); found in 37 birds, Ohio and eastern Indiana. Song 6.—Type 4bd-4 (15558-36); found in 41 birds, Ohio (Lake Erie to the Ohio River). Song 7.—Type 4fc-7 (15558-54); found in 26 birds, Ohio (Lake Erie to the Ohio River). Song 8.—Type 4bf-8 (15558-53); found in 50 birds, Ohio and West Virginia. Song 9.—Type 4fe-2 (15558-56); found only in this bird. Song 10.—Type 4bc-13 (15560-3); found in 24 birds, central and southern Ohio. Song 11.—Type 4hb-11 (15560-47); found in 30 birds, Ohio and Jackson County, Illinois. Song 12.—Type 3ae-5 (15560-60); found in 41 birds, Ohio, Kentucky, and West Virginia. Song 13.—Type 4hc-7 (15569-2); found in 19 birds, central and southern Ohio.

This classification greatly facilitated determining whether a newly recorded song type had been recorded before. This classification is artificial; I have no evidence that song types in a particular group are used in particular situations.

A White-eyed Vireo sometimes utters single short notes (like the first note of their Group 4 song types) between songs; these were not counted

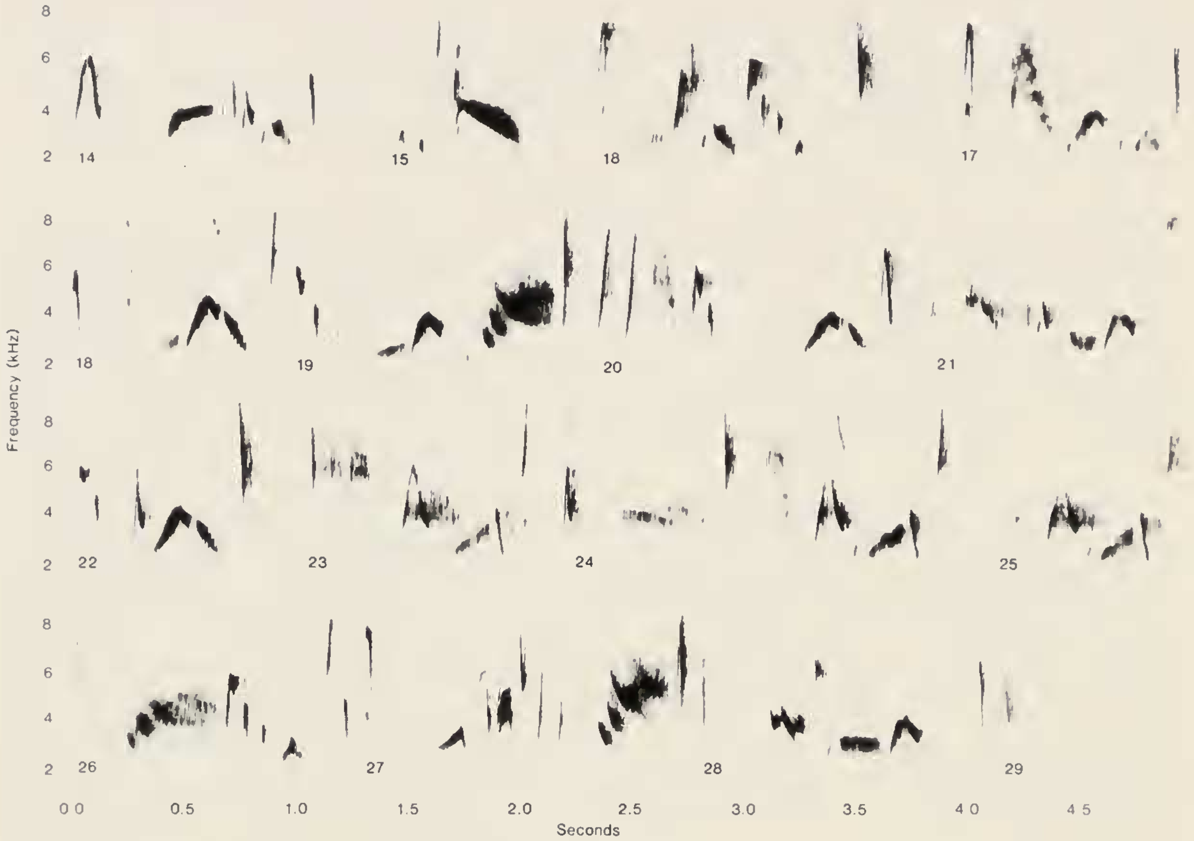

FIG. 2. Sonagrams of the song types of White-eyed Vireo No. 102, Zaleski State Forest, Vinton County, Ohio, June 1980. This bird's territory was about 400 m from that of bird No. 101. Song 14.—Type 4bc-13 (15570-14); see song 10. Song 15.—Type 2a-1 (15570-17); found only in this bird. Song 16.—Type 4e-23 (15575-2); found in 46 birds, central and southern Ohio. Song 17.—Type 4g-2 (15570-2); found in 11 birds, central and southern Ohio. Song 18.—Type 4fc-7 (15564-28); see song 7. Song 19.—Type 1b-4 (15564-44); found in 4 birds, (2 CCV, 2 ZSF). Song 20.—Type 2b-10 (15573-3); found in 6 birds, central and southern Ohio. Song 21.—Type 3ae-5 (15573-11); see song 12. Song 22.—Type 1g-4 (15573-23); found in 24 birds, 22 in Ohio, 1 in Chincoteague, Virginia, and 1 in southwestern Kentucky (Land Between the Lakes). Song 23.—Type 4g-10 (15575-5); found in this bird, another in ZSF, and a bird in BOSP. Song 24.—Type 4hb-6 (15575-21); found in this bird and a bird in Franklin County, Ohio. Song 25.—Type 3af-7 (15575-30); found only in this bird. Song 26.—Type 4hc-3 (15575-13); found in 6 birds, central and southern Ohio. Song 27.—Type 4bf-8 (15577-17); see song 8. Song 28.—Type 4c-25 (15581-1); found in 6 birds, central and southern Ohio. Song 29.—Type 4ha-1 (15575-27); found in 28 birds, 27 in Ohio and 1 in Wakulla County, Florida.

as songs. One bird (from Hb) uttered a note a little like the *wheep* note of a Great Crested Flycatcher (*Myiarchus crinitus*) (like the second note in song 8) (Fig. 1) about a second before some songs of two different types; these were not counted as songs.

The only instance I found of a 1-note song was in bird No. 101 (song 4) (Fig. 1). This was sung in series, like the bird's other song types, and appeared in three of the seven recordings I made of this bird (it appeared

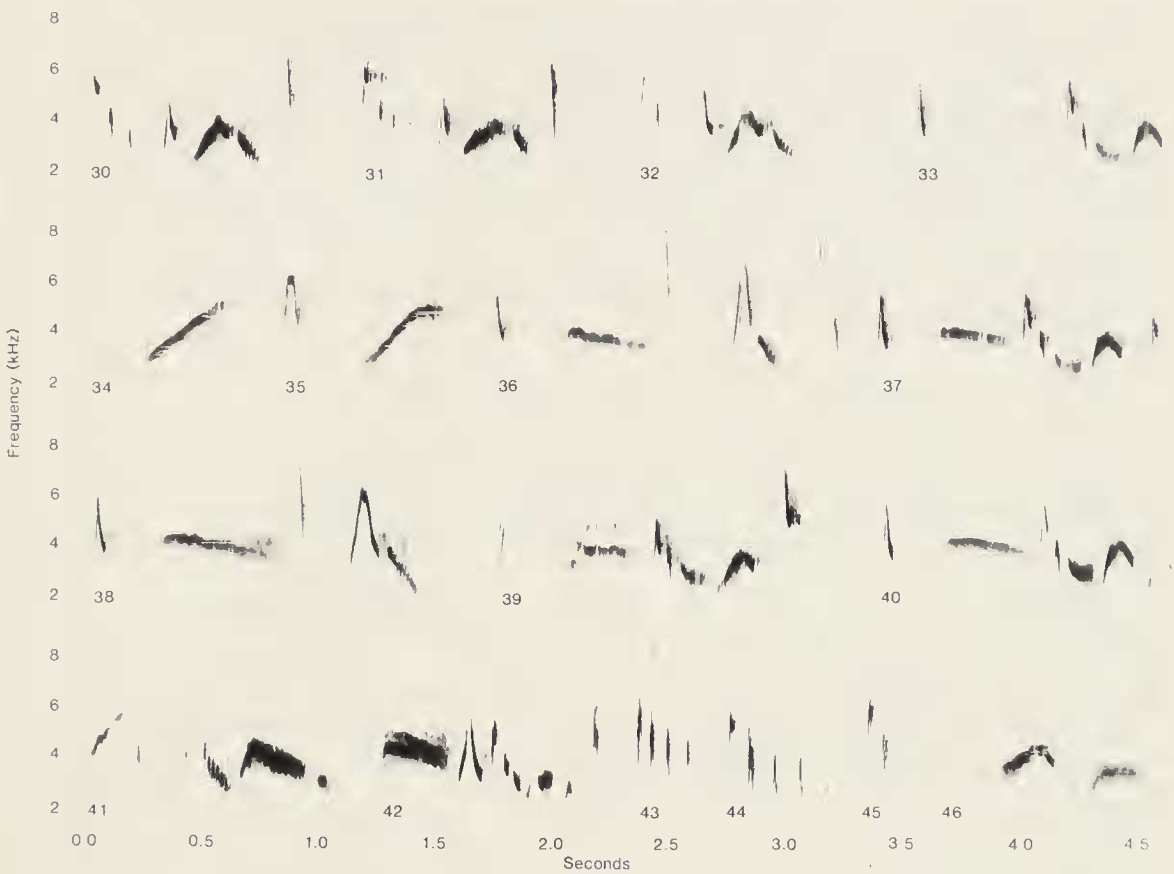

FIG. 3. Sonagrams of White-eyed Vireo songs (songs 30–42 and 46) and Summer Tanager calls (43–45). Song 30.—Type 1g-4 (14863-95), bird 125, SSF (see also song 22). Song 31.—Type 1g-4 (13523-2), bird 141, Land Between the Lakes, Kentucky. Song 32.—Type 1g-4 (14769-2), bird 147, Chincoteague, Virginia. Song 33.—Type 4hc-7 (15144-119), bird 27, BW (see also song 13). Song 34.—Type 4bc-1 (4434-4), bird 176, Tallahassee, Florida. Song 35.—Type 4bc-1 (N. C. St. Mus., 2-6), bird 151, Raleigh, North Carolina. Song 36.—Type 4hb-3 (14054-2), bird 210, Wakulla County, Florida. Song 37.—Type 4hc-7 (14863-11), bird 125, SSF. Song 38.—Type 4hb-3 (15890-6), bird 318, Hb. Song 39.—Type 4hc-7 (14054-8), bird 210, Wakulla County, Florida. Song 40.—Type 4hc-7 (15062-69), bird 126, SSF. Song 41.—Type 5ab-7 (1640B-15), bird 260, Bradenton, Florida. Song 42.—Type 5b-7 (11938-2), bird 208, Wakulla County, Florida. Call 43.—Summer Tanager (4141-2), CCV. Call 44.—Summer Tanager (15566-2), ZSF. Call 45.—Summer Tanager (15566-3), ZSF. Song 46.—Type 4be-2 (12979-2), bird 43, DCP; found only in this bird.

in two parts of one recording). This is unlike any other song or note of this species that I have ever heard or recorded.

Two-note songs (e.g., songs 34, 35) (Fig. 3) were found on 36 occasions, and involved 21 different song types. In 32 of these occasions the 2-note songs appeared to be short versions of a longer song, but in the other 4 occasions (involving two song types, 4bc-1, songs 34–35 of Fig. 3, and 5aa-2) did not.

Song types in Group 4 were the most common, comprising over half (54.7%) of the types found, and an even larger percentage (63.9%) of the songs studied; over three-fourths of the birds studied (307, or 81%) had one or more song types in this group. Types in Groups 2 and 5 were the least common, comprising only 11.2% of the types found, and an even smaller percentage (5.4%) of the songs studied. On the average, the birds studied used their types in Groups 1–3 in proportion to the number of types they had, but used types in Group 4 more, and types in Group 5 less. Only five of the 379 birds studied (1.3%) had song types in each of the five groups.

Song-Type Repertoires in Individual Birds

A White-eyed Vireo usually sings songs of one type for a while, then changes to another. In the 46 recordings I made containing 100 or more songs, the birds changed song types, on the average, every 3.66 min, but this varied from 1.0 to 9.3 min. If these birds sang at the rate of 12.62 songs/min (the average found; see below), the birds would sing from about 13 to 118 (average, 46) songs before changing to another type. (Barlow [1981] says that this species sings 50–100 songs of one type before changing to another.) If one recorded consecutive songs from a bird singing like this, he would need to record several hundred, perhaps over a thousand, songs before he could be reasonably sure he had all or most of the bird's repertoire. On the other hand, if he recorded like I did—recording a minute or so and then turning the recorder off until the bird changed songs—he would not need as many recorded songs to determine the bird's repertoire.

Fifty-five of the birds studied were represented by over 100 songs; their average repertoire was 11.7 song types and 15.3 variations. In general, for these birds, the more songs studied, the more song types were found. This correlation was significant ($r = 0.60$, $t = 4.96$, $P < 0.001$) for the 55 birds, but for the 15 birds represented by over 200 songs the correlation between the number of songs studied and the song types found was not significant ($r = 0.4483$, $t = 1.8081$, $P > 0.05$). The 29 birds represented by over 150 songs averaged 12.6 song types, the 15 with over 200 songs averaged 13.7 song types, the 11 with over 250 songs averaged 13.4 song types, and the 5 birds with over 300 songs averaged 14.8 song types.

The above analysis suggests that, using the recording techniques that I used, it would be desirable to have a sample of 200 or more songs to get all or most of a bird's repertoire. As the 15 birds in this study that were represented by over 200 songs had an average of 13.7 song types and 18.3 variations, these figures may be a reasonable estimate of an average vocal repertoire for individuals of this species. (Barlow [1981] gives 10–15 as the song-type repertoire size in this vireo.) Some individuals may have as many as 17 song types, and some may have as few as 10 (bird No. 343, ZSF, represented by 253 songs, had only 10 song types).

A Bird's Use of Its Song Types

Passerines with a repertoire of two or more song types use their repertoire in different ways. Some, including the Song Sparrow (*Melospiza melodia*) (Borror 1965), Carolina Wren (*Thryothorus ludovicianus*) (Borror 1956), Rufous-sided Towhee (*Pipilo erythrophthalmus*) (Borror 1975), Cardinal (*Cardinalis cardinalis*) (Lemon 1967), and others, usually sing songs of one type for a while and then change to another; a few, such as the Red-eyed Vireo (*Vireo olivaceus*) (Borror 1981) and Wood Thrush (*Hylocichla mustelina*) (Borror and Reese 1956), sing their songs in a varied sequence, rarely if ever singing the same song type two times in succession. The White-eyed Vireo is a passerine of the first type (i.e., it generally sings songs of one type for a while, then changes to another); when it changes song types, it may do so abruptly, or it may alternate song types for a few songs.

A few passerines sing songs of two types more or less alternately. This occurs in some species that have only two or three song types, such as certain flycatchers (Borror 1967), and it occurs occasionally in species with larger repertoires. It has been reported in the Song Sparrow (Borror 1965) and the Rufous-sided Towhee (Borror 1975), and it occurs occasionally in the White-eyed Vireo. In the case of the vireo, the song types used in alternate-type singing may be the same or different on different occasions, and the song types involved may also be sung in series by themselves. I do not know what significance, if any, song type alternation has in this vireo.

In a few of the wood warblers (Emberizidae, Parulinae), each bird has a repertoire of two song types, one of which is used primarily as an advertising song and the other chiefly in aggressive situations (Borror and Gunn 1985); this is the case in the Black-throated Green Warbler (*Dendroica virens*), the Golden-cheeked Warbler (*D. chrysoparia*), Townsend's Warbler (*D. townsendi*), and probably others. I have no evidence that the different song types of a White-eyed Vireo are used in different situations; a bird may respond to a given playback with different songs on different occasions.

Fifty-four of the 379 birds studied were recorded two or more times: 37 were recorded twice, 13 three times, 2 seven times, and 1 each eight and nine times. In most of these birds the sequence with which the birds' song types were sung differed in the different recordings; the exceptions involved short recordings with only two or three song types. There were no recordings with fewer than 100 songs that contained a particular song type early in the recording and again later in the recording. In the 46 recordings that contained over 100 songs, there were 16 in which one (5 recordings), two (6 recordings), three (2 recordings), four (2 recordings), or five (1 recording) song types appeared in two different parts of the recording; the second series of a song type came from one-half hour to about two hours after the first series.

It appears then, that in a given bout of singing, a bird will go through most of its song repertoire before repeating a song type, and this repetition may come from one-half to two hours after the first utterance of that song type. The different song types in a bird's repertoire are generally not sung in the same sequence on different occasions.

Playbacks of White-eyed Vireo songs were used in obtaining most of the longer recordings I made. Only one type (type 4be-2, song 46, Fig. 3, which was found in only one bird studied) was used prior to 1982. In 1982 two types were used, 4be-2 and 4e-22 (song 2) (Fig. 1), the latter a type found in 41 birds. In 1983 two types were used, 4be-2 and 1e-9 (song 1, Fig. 1, found in 29 birds). In 1984 and 1985 only type 4be-2 was used. The playbacks nearly always induced the bird to sing. No bird with which 4be-2 songs were used ever responded with songs of that type. Birds with which 4e-22 and 1e-9 songs were used responded with a variety of song types, but only rarely with the same type as the playback. Apparently this vireo only rarely responds to a playback with songs of the same type as the playback, and then only if it has that song type in its repertoire.

Singing rates were calculated from data on the average interval from the beginning of one song to the beginning of the next (termed "cadence" by Reynard 1963), in 63 birds (recorded in 1982, 1983, and 1984, with 6979 intervals). These rates varied from 4.4 to 23.7 songs/min, and averaged 12.62 ± 0.04 songs/min (Reynard 1963 gives the average cadence of 23 White-eyed Vireos as 5.1 sec, which is equivalent to 11.8 songs/min). In 47 birds there were some series preceded by playbacks, and others without playbacks; in 23 of these 47 birds the singing rate was significantly higher following playbacks, in 7 birds it was significantly lower in series preceded by playbacks, and in the other 17 birds the difference in singing rate with and without playbacks was not significant. Overall in these birds, the rate following playbacks ($\bar{x}$ = 13.06 ± 0.05 songs/min) was significantly higher than without playbacks ($\bar{x}$ = 12.25 ± 0.05 songs/min) ($P <$ 0.05). In my studies of Song Sparrows in Maine (Borror 1965), I found a somewhat greater increase in singing rate following playbacks, from about 5 to 8 songs/min.

Song Similarities in Different Birds

One may judge the similarities in the songs of different birds by the amount of sharing of song types or note types. Bradley's study of song variation in a Florida population of White-eyed Vireos (1981) was concerned with notes rather than song types. Each note type he found (sometimes note groups) was assigned a 2-letter designation, and each song was designated by a series of these 2-letter terms. Using computer analysis, he obtained values representing the differences between two or more songs or song repertoires. My studies of song similarities in different birds differed from those of Bradley in that I was concerned with the amount of song and note type sharing in different birds. I recognized 614 song types and 375 note types in the songs I studied, which would indicate that there is more variation and less sharing in song types than in note types.

Song type sharing.—Of the 614 song types found, 470 (76.5%) were found in only one bird. The birds studied admittedly represent a relatively small sample of the species population, and come from widely separated localities, but even in areas where considerable recording was done there were a great many unshared song types (Table 1). In one Ohio area (ZSF), where over 3800 songs were recorded from 35 birds, about a third of the song types found were found in only one bird, while in the eight other relatively well studied Ohio areas the proportion of song types found in only one bird ranged from about 17% (CCV) to >50% (DCP) of the song types found. In the case of the different subspecies, the more recording done, the fewer unshared song types were found.

The number of birds in an area having one or more song types shared with other birds was highest where the most recording was done. Of the 379 birds involved in this study, 273 (72.0%) had at least one song type shared with other birds, but in Ohio 183 of the 186 birds studied (98.4%) had at least one song type shared with other birds. This percentage differed in the five subspecies, and may reflect the degree of isolation of the birds involved: *novaboracensis,* 91.9%; *griseus,* 57.3%; *maynardi,* 23.1%; *micrus,* 11.8%; and *bermudianus,* 0.0% (song types found in the one individual of this subspecies studied were found only in this bird).

About two-fifths (59) of the 144 shared song types were shared by only two birds, but 15 types were shared by from 19 to 50 birds. A few song types in this species are found in many individuals, but most are found in only one or a few individuals.

Information on the relation between distance apart and the amount of song type sharing was obtained from two sets of data: (1) the sharings of the song types of the 36 Ohio birds that had ten or more song types, and (2) the sharings of the song types of all the birds recorded in the nine most studied Ohio areas. As these two studies showed essentially the same thing, only the latter is reported here.

For each song type found in each of these nine areas, counts were made of the numbers of birds, at various distances, that shared the type; these numbers were added to produce a set of totals for each area, and the area totals were added to produce a grand total for the nine areas. The figures for the different areas differed somewhat, due at least in part to the different numbers of birds studied in the different kilometers-away zones. Studies of the sharings of the song types of 36 Ohio birds produced sharing totals that were very similar for the birds in a given area, but differed in different areas. Adding the area totals produces figures that represent an average of all nine areas. Over half of the song-type sharings in these birds occurred in birds over 80 km away (58.3% in Zones 4 and 5, 81–320 km away), while less than one-tenth (9.1%) occurred in birds in the same area (Zone 1). Beyond 320 km (Zones 6 and 7) the sharings dropped off considerably, but there was at least some sharing by birds over 800 km away.

Some of the differences in the percentage figures in Table 4 may be due to differences in the numbers of birds studied in the different distance-away zones; to take this into account, calculations were made of the number of sharings per bird studied in each distance-away zone. These figures are given in the *s/b* lines in Table 4. For all nine areas (bottom line of Table 4) these figures are similar for Zones 1–5, but a little higher in Zone 4, and a little lower in Zones 3 and 5, and considerably lower for Zones 6 and 7.

The data on song type sharing in this vireo suggest that in a bird with 13 or 14 song types (near an average for this vireo), one might expect two or three of these song types to be unique (found only in that bird), and the rest shared with other birds. Of the shared types, one would expect two or three to be shared with other birds in the same area, and the rest shared with birds outside the area. In the case of a bird's song types that were shared by birds outside its area, one would expect that at distances up to 320 km away, about one bird in five would share one or more of its song types, but beyond 320 km the sharings would drop off considerably. Of the sharings found, one would expect most to be with birds 80–320 km away, and at least one would be with a bird over 800 km away.

The higher percentage of shared song types in well studied areas than in more separated areas (e.g., 37.1% for the nine Ohio areas represented in Tables 1 and 4, and 23.5% for all birds studied) may reflect the degree of isolation of many of the birds studied. Large samples in well-studied areas contain fewer unique song types than small samples from widely separated areas. There is little evidence of distinct local dialects in this vireo, but song similarities are greater in populations less than 320 km apart than in more widely separated populations.

The song-type sharings by birds over 800 km apart involved seven different song types: (1) Type 1g-4: found in 22 Ohio birds, a bird in Chincoteague, Virginia, and a bird in southwestern Kentucky (songs 22, 30, 31, 32) (Fig. 2, 3). (2) Type 3c-6: found in 6 Ohio birds and a bird in

TABLE 4
SHARING OF THE SONG TYPES IN NINE OHIO AREAS

Area[a]	No. of birds	No. of shared song types[b]	Item[c]	Distance-away zones[d] 1	2	3	4	5	6	7	Total sharings
Cast	10	20	%	2	<1	—	10	71	17	<1	449
			s/b	0.8	1.0	—	3.1	2.4	1.4	0.01	
DWA	6	12	%	2	17	4	61	16	1	—	258
			s/b	0.8	2.0	0.5	1.4	1.2	0.1	—	
Hb	8	31	%	4	13	20	44	19	1	1	558
			s/b	2.8	2.7	1.8	3.9	3.0	0.2	0.02	
BW	14	29	%	6	19	13	38	23	1	<1	541
			s/b	2.3	2.3	1.8	4.3	2.7	0.2	0.01	
DCP	12	20	%	3	15	22	36	23	1	1	396
			s/b	1.1	1.8	1.9	2.6	2.0	0.1	0.01	
CCV	35	38	%	10	11	53	20	5	1	<1	568
			s/b	1.7	2.4	3.8	3.2	1.9	0.2	0.01	
ZSF	35	53	%	26	9	17	42	5	1	1	630
			s/b	4.7	4.2	2.1	3.4	2.1	0.1	0.02	
BOSP	10	29	%	5	44	4	42	5	1	<1	536
			s/b	2.5	3.3	1.2	2.8	1.9	0.1	0.01	
SSF	29	46	%	14	—	1	58	23	5	1	602
			s/b	2.9	—	1.0	3.3	3.2	0.6	0.02	
Total	159	278	%	9	14	16	38	20	3	<1	4538
			s/b	2.6	2.6	2.2	3.0	2.4	0.4	0.01	

[a] Abbreviations for the Ohio areas are explained in the text.
[b] The number of song types for which counts of sharings were made.
[c] Percent of the total sharings of the song types in the area found in the zone, and the number of sharings per bird (*s/b*) studied in the zone.
[d] Zone 1, the same area (<16 km away); Zone 2, 16–48 km away; Zone 3, 49–80 km away; Zone 4, 81–160 km away; Zone 5, 161–320 km away; Zone 6, 321–800 km away; Zone 7, >800 km away.

Wakulla County, Florida. (3) Type 4bc-1: found in 3 birds—in Raleigh, North Carolina, Leon County, Florida, and Gainesville, Florida. (4) Type 4e-20: found in 5 birds, 4 in Wakulla County, Florida, and 1 in eastern Maryland (Willards). (5) Type 4ha-1: found in 29 Ohio birds and a bird in Wakulla County, Florida (song 29) (Fig. 2). (6) Type 4hb-3: found in a Central Ohio bird, a bird in Northampton County, North Carolina, and a bird in Wakulla County, Florida. (7) Type 4hc-7: found in 18 Ohio birds and a bird in Wakulla County, Florida (songs 37, 39, 40) (Fig. 3).

Two of these seven song types (4bc-1 and 4ha-1) might possibly be considered short versions of a longer type. Type 4bc-1 contains only two notes (songs 34, 35) (Fig. 3), like the first two notes in several other song types. Type 4ha-1 contains three notes (song 29) (Fig. 2), and several song types begin with these three notes. The Florida bird that sang 4ha-1 songs sang only one song of this type, plus two longer songs beginning with these same three notes; in the Ohio birds with this song type it was sometimes sung more or less alternately with a longer song beginning with these same three notes, and sometimes in a series by itself.

The other five song types sung by birds over 800 km apart were longer songs (see songs 33, 37, 39, 40, and 36, 38) (Fig. 3), and any differences in length (e.g., songs 36 and 38) were minor and of a type encountered in many individual birds.

Note type sharing.—There were many fewer note types than song types in the birds studied (375 note types, compared with 614 song types), and much more sharing of note types than of song types. Of the 375 note types found, 118 (31.5% were found in only one bird; 76.5% of the song types were found in only one bird), and the shared note types were found in from 2 to 225 birds (shared song types in 2 to 50 birds).

Most of the note types that were found in only one bird were found in more or less isolated areas; there were relatively few unshared note types in the songs of birds in well studied areas. For example, of the 80 note types found in CCV birds, none was found in only one bird, and in the SSF birds, where 90 note types were found, only two types were found in a single bird studied (Table 1).

Information on the relation between distance apart and the amount of note type sharing was obtained in the same way as for song types. The total percentage figures for the sharings of note types in nine Ohio areas (comparable to the % line at the bottom of Table 4) were as follows: Zone 1, 6.5%; Zone 2, 9.9%; Zone 3, 11.2%; Zone 4, 26.9%; Zone 5, 15.9%; Zone 6, 6.3%; and Zone 7, 23.2%. The corresponding *s/b* figures for the seven zones (comparable to the last line in Table 4) were: Zone 1, 19.4; Zone 2, 19.9; Zone 3, 17.2; Zone 4, 21.9; Zone 5, 20.0; Zone 6, 10.1; Zone 7, 7.7. The figures on sharing of note types are similar to those for song types, but with a smaller percentage of the sharings in the nearer zones and more in the distant zones. The *s/b* figures on note type sharings are very similar to those for song type sharings: very similar in Zones 1–5, with a noticeable drop in Zones 6 and 7.

Geographic Variation

Five subspecies of the White-eyed Vireo occur in the continental United States and neighboring islands: *V. g. novaboracensis, V. g. griseus, V. g. maynardi, V. g. bermudianus,* and *V. g. micrus. V. g. novaboracensis* occurs throughout the northern part of the species' range, east to the coastal plain areas of Virginia, the Carolinas, and Georgia, and South to about the middle of the Gulf states; *griseus* occurs from central Texas eastward through the southern portions of the Gulf states, northern Florida, and up the east coast; *maynardi* occurs in peninsular Florida, from Tampa Bay south, and in the Bahamas; *bermudianus* occurs in Bermuda; and *micrus* occurs in southern Texas.

The recordings I studied come from a large section of the species' range in the United States and represent all five subspecies, but the numbers of birds and songs from many areas are probably too small to give an adequate picture of the songs in those areas (Tables 2 and 3).

The data in Table 2 show a tendency toward a decrease in song length and the number of notes in the song going from north to south, but the songs of *griseus* in central Texas averaged longer and contained more notes than songs from most other areas. There was little variation in the average note length in songs from different parts of the country (Table 3), but the notes of Texas birds (*griseus* in part, and *micrus*) averaged shorter than those in songs elsewhere. In general, the proportion of a bird's notes that were very short (≤0.05 sec), decreased going from north to south, but short notes were more common in Texas birds than in most others. The relative number of birds with long notes in their repertoire (≥0.3 sec) tended to decrease going from north to south, and was lowest in Texas birds and in the *griseus* from the southeastern states. On the average, 5.0% of the notes of the birds studied were long notes (≥0.3 sec); this percentage was highest in *novaboracensis,* and lowest in Texas and Bermuda birds.

The incidence of song types in the five major groups differed somewhat in different parts of the country. Songs of types in Group 1 were more common in most of the South than in the North, and types in Group 4 were less common. Songs of types in Group 3 were more common in the deep South (southern Florida and southern Texas) than elsewhere. Song types in Group 2 were moderately common in the Southeast, but were less common in the South than in the North. Song types in Group 5 occurred more often in the southern states than elsewhere.

V. griseus is divided into subspecies on the basis of differences in color; I would not divide it into subspecies on the basis of song.

DISCUSSION

My findings agree fairly well with those of Bradley (1980, 1981), though we approached song variation somewhat differently. Bradley (1981: 82) gave the average song length as 1.02 sec (N = 213), while the songs I studied (N = 16,612) averaged 1.10 sec in length (1.05 sec for 1799 songs from Gainesville; Bradley apparently based his figures on the song types found, rather than on all the songs he studied). We both found that a bird responding to playbacks does not attempt to match the song type of the playback. His finding of a lack of correlation between the song (element) similarity and distance apart in a local area agrees with my findings (for song and note types) over a larger area.

None of the birds I recorded was color banded or otherwise marked for individual identification, but most of my recordings (and probably all of the Ohio recordings) were made during the nesting season—and recordings made in a given territory during the same season were assumed to be of the same bird. Conversely, recordings made in different territories were assumed to be of different birds. As no two birds studied had the same song-type repertoires, this repertoire may also serve as a means of individual identification. Birds whose territories are close together may share a few song types, but only a few. Birds 101 and 102, which were recorded the same week in June, 1980, about 400 m apart, shared four song types: songs 7 and 18, 8 and 27, 10 and 14, and 12 and 21 (Fig. 1, 2); their other song types were different.

Although a human observer may learn to recognize individual White-eyed Vireos by their song-type repertoire, I do not know whether or not individual vireos can do this. There is much experimental evidence (Falls 1982) indicating that many birds can recognize other individual birds by their songs (or at least distinguish between neighbors and strangers); this ability appears more pronounced in species in which each individual has only one song type; as repertoire size increases, this ability appears to decrease (Falls 1982). It has been suggested that in birds with a sizeable song type repertoire a bird may sing its most distinctive songs more frequently, but this does not appear to be the case in the White-eyed Vireo. (This point was checked in 36 Ohio birds that had one or more unique song types, and were represented by either 100 or more songs or had 10 or more song types. In these 36 birds, on the average, 20.8% of their song types, but only 18.8% of their songs, were unique; these birds averaged 16.3 songs per type of their unique types, and 17.3 per type of their shared types.) My playbacks of White-eye songs to White-eyes in the field were designed to increase their singing, not to determine the bird's ability to distinguish between different songs.

Most of my recordings of White-eyed Vireos were made in a few areas, over a period of several years. I have frequently recorded a bird in the same place in successive years, but I have only once found a bird that I thought was the same bird I had recorded there the previous year. Bird 329 was recorded in the same area in 1982 and 1983 (in BW); 13 of its 17 song types were sung both years. This bird sang 14 song types in 1982 (1 not sung in 1983), and 16 types in 1983 (3 not sung in 1982). I believe the fact that 13 song types were sung in this area both years indicates that the same bird was there both years. Seven of the 17 song types sung by this bird were not found in any other bird studied.

Song variation in this vireo is much like that in the Song Sparrow (i.e., each bird has a repertoire of several song types, and sings one for a while and then changes to another). In my study of Song Sparrows in Maine (Borror 1965), I found very little song type sharing by different birds (but considerable note type sharing), but I did find a number of instances of individual birds (identified by their song type repertoires) returning to approximately the same territory in successive years.

Studies of banded birds have shown that many birds return to a given nesting area in successive years. Barlow (pers. comm.) found Gray Vireos (*V. vicinior*) returning to breeding areas in western Texas as many as four years in a row, and he found Black-capped Vireos (*V. atricapilla*) returning in successive years to breeding territories in Texas and Oklahoma. I have no information on recoveries of banded White-eyed Vireos returning to the same breeding areas in successive years, but Rappole and Warner (1980) report banded White-eyed Vireos returning to the same wintering area in Mexico in successive years.

There are three possible reasons why I did not find more instances of White-eyed Vireos returning to the same breeding area in successive years: (1) they seldom return to the same territory because of a high over-winter mortality; (2) they return to a different territory; or (3) they may return to the same territory, but have changed song types and I do not recognize them. The first possibility seems unlikely, as I see no reason why White-eyed Vireos should have higher over-winter mortality than do Song Sparrows, Gray Vireos, or any of the other species in which returning to the same territory in successive years has been shown by banding. Barlow (pers. comm.) reports instances of banded Gray Vireos returning to the same territory, in which they sang different song types in successive years. As my birds were not banded, I have no way of checking this possibility in my birds, but because of my experience with other species, I doubt that a White-eyed Vireo would change its song types from one year to the next.

Two intriguing questions arise with this vireo—as well as in many other passerines: (1) just how does a bird come to sing the particular song types that it sings, and (2) how can one explain the geographic distribution of song types that he finds. In many species, including this vireo (Bradley 1981) there is evidence that some songs, or some features of the songs, are learned from males in the area where the bird was reared. If this is a significant method of song acquisition in the White-eyed Vireo, we would expect to find (in a nonmigratory population, or in one returning to the same area in successive years) the song similarities greater the closer together the birds were. This does not appear to be the case in the White-eyed Vireo, either from my study or that of Bradley (1981). (Bradley was dealing with a nonmigratory population, while most of my birds were form migratory populations.)

The songs of a White-eyed Vireo (and of other species as well; see Borror 1981) are very variable before the types become fixed—as though the birds were experimenting with different note types and sequences—and the particular song types that become fixed and in the primary song repertoire may be to some extent a matter of chance, with perhaps in some species a tendency for the bird not to duplicate too closely the songs of its neighbors.

The higher percentage of the song type sharings in Zone 4 (81–160 km away) (Table 4) appears to be due to the larger numbers of birds studied in that zone. Figures on the number of sharings *per bird studied* (*s/b* figures in Table 4) show only a slight increase in the sharing in Zone 4. The *s/b* figures in Table 4 show a similar amount of song type sharing up to a distance of 320 km.

Attempts have been made to explain the geographic distribution of song types of birds (see Lemon et al. 1985), but most of the factors suggested do not appear to have been important in the case of the White-eyed Vireo, principally because each male of this vireo has a repertoire of song types that differs in character and distribution (see Fig. 1, 2). It is probable that the distribution of White-eyed Vireo song types reflects only the effects of chance, with no direct selection involved (as suggested by Slater et al. 1980 for the Chaffinch [*Fringilla coelebs*]). The "chance" factor in this vireo has probably been affected by the mechanism of song acquistion (through the influence of neighboring males in the area where the bird was reared) and the apparently uncommon return of a bird to the same area in successive years.

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